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# Male mate choice, sexual conflict and strategic allocation of copulations in a lekking bird

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The males of lekking species are not expected to be choosy about mating because a reduced reproductive rate due to lost mating opportunities should outweigh any benefits of male choice. Females have traditionally not been expected to be competitive in this system since their reproduction has usually been assumed to be unconstrained by male availability. Here we show that, in contrast to these predictions, males are choosy and females may be competitive in the lekking great snipe *Gallinago media*. Males preferred by many females often refused to copulate with and even chased away females that the male had already copulated with, whereas females seemed to compete for repeated copulations. We conclude that choosiness may sometimes pay for popular males in those lekking species where females copulate repeatedly. Apparently, evolutionary conflicts of interest between individuals may cause a richer repertoire of behavioural adaptations than, to our knowledge, hitherto realized.

**Keywords:** male mate choice; sexual conflicts; lekking; copulation behaviour; great snipe; *Gallinago media*

## 1. INTRODUCTION

Lek systems, where only females care for the offspring, excess males are available on display arenas and pair bonds are virtually non-existent, are celebrated for exhibiting strong male competition and strong female mate choice (Höglund & Alatalo 1995). Theoretical models have predicted that males should not be choosy in this system because a reduced reproductive rate due to lost mating opportunities should outweigh any benefits of male choice (Deutsch & Reynolds 1995; Johnstone *et al*. 1996). On the other hand, females are thought to have little to lose by being choosy and even slight benefits of mate choice may therefore have favoured its evolution (Reynolds & Gross 1990). Male competitiveness is expected because it may give an immediate reproductive benefit (Darwin 1871). Since females' reproduction is not thought to be limited by male availability in lek systems, females have traditionally been assumed not to be competitive, but this has been questioned (Berglund *et al*. 1993).

Competition and choice are not necessarily opposite sex roles (Owens & Thompson 1994; Owens *et al*. 1994). Both sexes may show flexibility in their competition for mates and mate choice. Females in some lekking species copulate repeatedly with the same male and even more so if other females are present (Petrie *et al*. 1992; Fiske & Kålås 1995). This phenomenon may be explained as a consequence of female competition for ejaculates (Petrie *et al*. 1992; Hunter *et al*. 1993). Here, we explore males' responses to repeated copulation by females, given that sperm is a limited resource (e.g. McCartney *et al*. 1958; Dewsbury 1982; Birkhead 1991). We present analyses of a large dataset on mating solicitations by individual colour-ringed great snipe (*Gallinago media*) females in order to understand the dynamics of the evolutionary conflicts of interest over copulations within and between sexes.

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## 2. METHODS

### (a) *Observations and data*

We studied a population of colour-ringed great snipes in Gåvålia, Norway, in 1994–1998 (for general methods see Fiske *et al*. 1994; Fiske & Kålås 1995; Sæther 1999; Sæther *et al*. 1999, 2000). Two to four leks were intensively monitored each year between 20 May and 15 June. Solicitations by females and their outcomes and the number of other females present at the territory when solicitations occurred were noted. Females solicit copulations by an easily recognized squatting behaviour. We defined a solicitation as resulting in copulation when cloacal contact was achieved. This was nearly always the case when a male mounted a soliciting female, but we could not be certain whether all copulations resulted in sperm transfer. We also noted the causes of female departures from male territories (Sæther *et al*. 1999), including chasing by other females and by the male territory owner. Females only visit leks during a few hours each night (Kålås *et al*. 1995). Individual females return for several nights and, after a period of mate sampling, usually solicit mating on more than one night (Fiske & Kålås 1995). Females depart and return to territories repeatedly during a single night, often due to harassment from neighbouring males (Sæther *et al*. 1999).

The total sample consisted of 1300 courtship visits by identified females to identified males in 1994–1998. These females made 550 mating solicitations, including 212 that led to copulation involving 105 'female years' (77 individuals) and 42 'male years' (27 individuals). The sample sizes of the males and females used in the analyses are 'bird years' (each bird was included once each year). Observations for each mating season are considered independent since we analyse variation in behaviour dependent on variation in the context within mating seasons. When analysing the number of solicitations and copulations for each female we excluded females not seen to copulate that year even if they had solicited. We also tried to avoid including females for which we could have missed observing the first copulation. In order to be included in the analyses, a female had to be either marked in a previous year or to have

been observed at least 1 day without soliciting before her first recorded solicitation. A few solicitations ($n=13$) were disrupted by neighbouring males (Sæther *et al*. 1999) and are excluded from all analyses.

### (b) *Analyses*

First, we tested whether there is any evidence for female competition for mates. We compared the females' solicitation and copulation behaviour when they were alone with a male with their behaviour when they were together with other females, a context that is of greater potential for a conflict of interest between females. We also analysed where aggressive interactions between females occurred. If females try to chase other females away because of competition for mates, the aggressive females should do this when in the territory of the male with which they prefer to mate and not when in the territory of other males. We tested whether this was the case by comparing the frequency of aggression in territories where the aggressive female copulated with the expected frequency of aggression by chance. This expected frequency was based on the proportion of female visits to territories where the individual female copulated.

Second, we tested whether there is any evidence for male mate choice. If males prefer copulating with new females rather than those with which they have already copulated, the probability of a solicitation resulting in copulation should be lower after a female has already copulated with the male. This should particularly be the case if other females are present on the territory because of a larger potential for a conflict of interest between the male and the female soliciting mating. We use logistic regression for analysing the effects of previous copulation with the same female and the presence of other females on the outcome of solicitations. In this analysis we also test for an effect of the number of previous copulations the same day, since sperm depletion could directly influence the probability of copulation. The number of previous copulations includes copulations with all females, also unmarked ones.

Males sometimes chase females out of their own territory (Sæther *et al.* 1999). We tested whether this behaviour was performed randomly towards females or, alternatively, towards females with which the male had previously copulated. We tested the observed pattern (the proportion of cases occurring after the female had copulated with the male) against expectations by chance in several ways. We first used the number of chases as the unit of measurement. However, since some males made several chases and some females were chased more than once, pseudoreplication questions the validity of the analysis. We therefore also made separate analyses using both the males involved and the females involved as the unit of measurement. If a female was observed being chased both after copulation and otherwise, she was counted as 0.5 in both states. We derived several null model distributions in order to test the observed patterns. In the simplest case we compared the frequency of chases occurring after copulation with an equal expectancy using sign tests. However, since females may not visit males equally frequently before and after starting copulating we also derived more realistic null models. These were based on observations of the females being in one of two states (previously copulated with the territory owner or previously not copulated with the territory owner). We measured the expected frequencies as the number of female visits, the amount of time spent in territories and the number of individual females observed. We then tested the observed pattern of chases against the expectations of the derived null model using binomial tests or randomization tests. The randomization simulations of the null model were based on the actual numbers of chases and null model observations for each bird. A single simulation involved counting the number of chases occurring by chance after copulating with the territory owner and this procedure was repeated 10 000 times. Randomization $p$-values were calculated as twice the frequency of the simulated test statistics that were greater than the observed test statistics divided by the number of simulations (see Sæther *et al.* (2000) for a similar approach).

We also report on data about females mating with more than one male in a single mating season in relation to the number of other females mating with these males. A male mating with more individual females than another male was defined as being more popular. We also included in this analysis data from the same leks during 1989–1993 (Fiske & Kålås 1995) in order to increase the sample size. We analysed whether females shifted from less popular to more popular males (e.g. if a more preferred male is only encountered later) or, alternatively, from more popular to less popular males (e.g. to ensure fertilization of all their eggs).

The statistical analyses were performed using Spss 6.1 and, for the randomization tests, Resampling Stats (Resampling Stats, Inc., Arlington, VA, USA). All $p$-values are two-tailed.

## 3. RESULTS

### (a) *Female competition for matings*

We have previously reported that females solicit mating and copulate more often when other females are present at the male's territory (Fiske & Kålås 1995). This result is confirmed by the analyses of the present, larger dataset. Females that were accompanied by other females solicited more often ($n=60$ females and median $=5$ solicitations) as compared with females that were always the sole female in the territory when their solicitations occurred ($n=28$ females and median $=3$ solicitations) (Mann–Whitney $U$-test, $z=-2.46$ and $p=0.01$). This resulted in more copulations occurring for females that were accompanied by other females (median $=2$ copulations) than for solitary females (median $=1$ copulation) (Mann–Whitney $U$-test, $z=-2.06$ and $p=0.039$). Moreover, females solicited mating and copulated more often when the male received solicitations from other females on the same day ($n=73$ females and median $=5$ solicitations with two copulations) as compared with females that were the sole soliciting female ($n=16$ females and median $=2$ solicitations) (Mann–Whitney $U$-test, $z=-2.57$ and $p=0.01$) (median $=1$ copulation) (Mann–Whitney $U$-test, $z=-2.29$ and $p=0.02$).

Females sometimes behaved aggressively towards other females. Aggression usually occurred within the territory where the aggressive female mated (81% of 21 cases). When compared with how often individual females visited the territories of males with which they mated as opposed to other males, this is more often than expected by chance alone (54.5% of 1255 visits) (binomial test, $p=0.02$).

### (b) *Male choosiness*

Solicitations resulted in copulation less often after the female had first copulated with a male. Overall, 69% of females' first solicitations ($n=70$) resulted in copulation,

but only 40% of solicitations resulted in copulation after the female had undergone one copulation with the male (median of the proportion for each female weighted by the number of solicitations). This result is as expected if males prefer copulating with new females to those with which they have already copulated. Logistic regression analysis (table 1) confirmed that solicitations led to copulation significantly less often if the pair had already copulated. The presence of other females in the territory was not important in itself in influencing the probability that a solicitation would lead to copulation. Instead, we found an interaction effect between the presence of other females and whether the pair had already copulated in addition to the effect of the latter. This shows that males often refuse further copulations with females with which they have already copulated, and more so if other females are present. A refusal to copulate could be a direct effect of sperm depletion or, alternatively, an adaptive strategy for saving sperm for new females despite having sufficient sperm stores for copulation. The former possibility is not supported by the data (table 1) because the number of previous copulations on the same day (with any female) did not improve the fit of the logistic regression model.

Table 1. Logistic regression analysis of the factors influencing whether a male would copulate with a soliciting female.

(Variables that are not in the model were removed by backward elimination of non-significant variables. Non-significant interaction terms are not shown. LR refers to the likelihood ratio. Already mated refers to whether the male had ($n = 195$) or had not ($n = 229$) previously copulated with the soliciting female in the current year. Other females present refers to whether other females were ($n = 191$) or were not ($n = 233$) present in the territory when the solicitation occurred. Number of copulations refers to the number of previous copulations by the male with any female the same night.)

| variable | $-2\log LR$ | $p$ |
|---|---|---|
| variables in the model | | |
| already mated | 19.42 | $< 0.0001$ |
| already mated × other females present | 5.72 | 0.017 |
| variables not in the model | | |
| other females present | 0.005 | 0.95 |
| number of copulations | 0.60 | 0.43 |

Males aggressively chased females away from the male's own territory, lending further support to the idea that males make strategic choices between females. As expected, this remarkable behaviour was performed almost exclusively towards females with which the male had already copulated (figure 1). The non-randomness in this pattern was robust when tested against several null models with divergent assumptions (figure 1). The data are conservative in the sense that we cannot exclude the possibility that the observers had missed the first copulation of the very few females that were recorded as chased away before copulation.

Females sometimes solicited additional copulations from other males, thereby suggesting that there are costs of not remating for males. In 69% of 13 cases, females shifted from a more popular to a less popular male (both males were always present). Low power prevented testing whether the pattern is non-random, but it nevertheless indicates that females may mate with additional males even if they have already found a superior one.

## 4. DISCUSSION

This is, to the authors' knowledge, the first report of males in a lekking species being choosy about copulating, as envisaged by Dewsbury (1982) almost 20 years ago (see also Avery 1984; Barnard & Markus 1989; Galvani & Johnstone 1998). Males preferred by many females did not indiscriminately copulate with any female soliciting, but appeared instead to allocate copulations strategically to females with which they had not yet copulated and also violently chased away females with which they had already copulated. This unexpected conflict of interest between a lekking male and a female soliciting copulations from him suggests that males have evolved behavioural adaptations for facing constraints on their sperm supply.

Male reluctance to copulate or transfer sperm has previously been described in animals without paternal care, but in these cases in relation to females that had copulated with another previous male (Schwagmeyer & Parker 1990; Suter 1990; Arnaud & Haubruge 1999) rather than the same male, as in the present study. Males unwilling to copulate with soliciting females have been observed in other lekking birds, but this has been dismissed as 'a result of males acknowledging the coyness of females' in order to avoid frightening off the female (Bradbury & Davies 1987, p. 150). That assertion now seems to be wrong.

Earlier theoretical and empirical work on the strategic allocation of sperm (e.g. Parker 1990*a*,*b*; Hunter *et al.* 2000; Nicholls *et al.* 2001) has focused on the conflict of interest between males that arises from females copulating with more than one partner, thereby causing sperm competition (Parker 1970, 1998). Here we focus instead on the strategic allocation of copulations because of another conflict of interest: that between males and females over the use of sperm. Although it may seem surprising that males would voluntarily reduce their mating opportunities as we describe here, this is expected from the conflict of interest between males and females that arises from mutual mate choice (figure 2*d*). The existence of this conflict rests on three assumptions: that sperm is a limited resource, that females try to copulate repeatedly with the same male and that males have the potential for mating with more than one female. So far we have no direct evidence regarding whether the first assumption holds true in this species, but the other two assumptions are well documented to be true (Fiske *et al.* 1994; Fiske & Kålås 1995; Sæther *et al.* 2000).

In some lekking species, females only copulate once per clutch (Alatalo *et al.* 1996). There is no basis for the conflict we describe to exist in this case. Hence, we do not expect males in those species to have evolved choosiness since the benefits of male choice based on any other quality differences among females (see e.g. Altmann 1997) are very unlikely to offset the costs in terms of a reduced reproductive rate (Deutsch & Reynolds 1995; Johnstone *et al.* 1996). However, females of a number of lekking bird

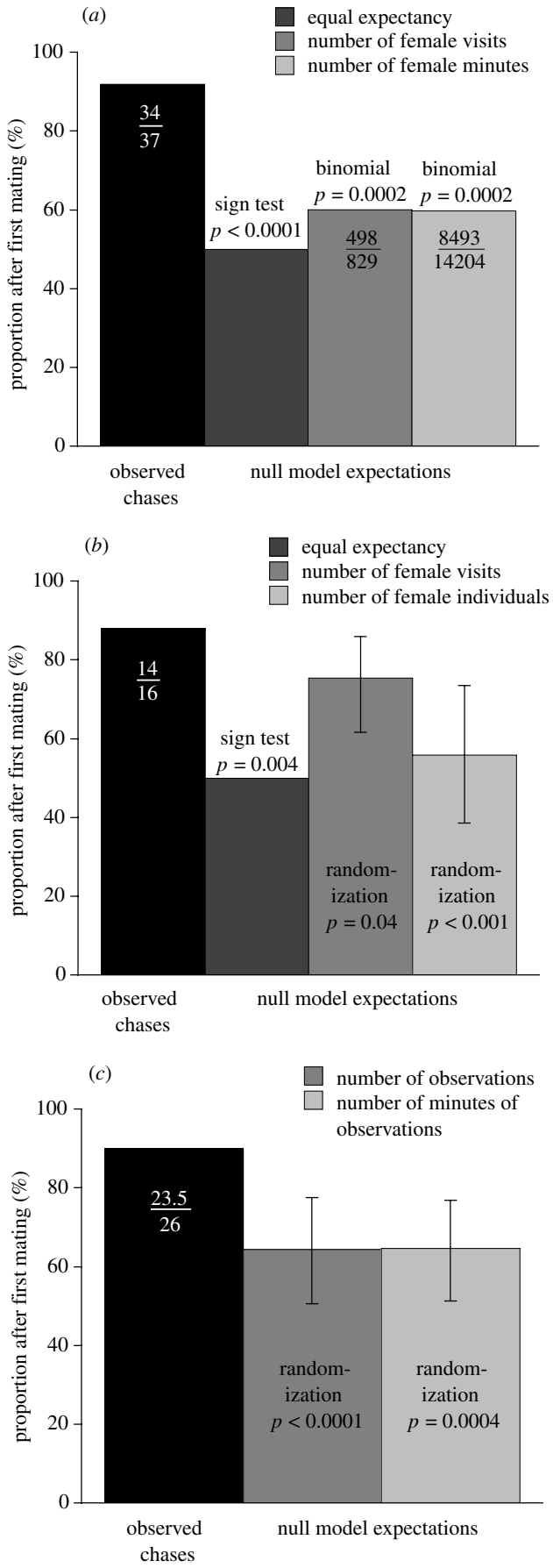


Figure 1. Females chased away from the territory by the male territory owner were more likely than expected by chance alone to have previously solicited copulation with the male. The observed values are the proportions of observations of females being chased by the territory owner that involved females having already solicited copulation with the male. In the remaining cases the female had not yet started mating with this male or never did so. The figure shows the results using (*a*) chases, (*b*) males involved and (*c*) females involved as the units of measure. Different null models are different ways of constructing an expected distribution in order to compare it with the observed distribution of when chases by the territory owner occurred. The expected values are the frequencies of observations occurring after mating in the null model distribution or the mean frequency of 10 000 simulations of a null model. In the latter case, 95% confidence limits are indicated.

species copulate repeatedly and we expect that the potential for conflict thus created may also have resulted in the evolution of male choosiness in other lek mating species. The reason why these adaptations have gone unnoticed until now need not only be due to a male-biased or narrow perspective on mating systems, but may also be because it has proved notoriously difficult to obtain information on individual females in lek systems.

We have assumed that copulation always involves sperm transfer. This is known not to be the case in some birds (Hunter *et al.* 2000) and could potentially complicate analyses. In particular, it could hide the strategic allocation of sperm from discovery. Hunter *et al.* (2000) were able to show that Adélie penguin (*Pygoscelis adeliae*) males were more likely to transfer ejaculates during copulations with extra-pair females as compared with their pair females and it is well established in several animals that males are able to allocate more sperm when facing a higher risk of sperm competition (Nicholls *et al.* (2001) and references therein). However, in the present case it seems that great snipe males are choosy about copulation itself, which cannot be explained by a failure to transfer ejaculates. On the other hand, it is possible that the observed pattern of repeated copulation by females is a consequence of biases in sperm transfer, instead of resulting from female competition. However, the pattern of aggression between females provides some support for the idea that females do compete for ejaculates (see also Pruett-Jones & Pruett-Jones 1990; Petrie *et al.* 1992; Karvonen *et al.* 2000).

Most females that copulated with additional males shifted from a more popular to a less popular male. This suggests that female promiscuity is not an adaptation for devaluing sperm from inferior males (Petrie 1992; Hunter *et al.* 1993) and may instead possibly be a consequence of male choosiness. Mating with popular males may entail costs for females as they may risk being left with unfertilized eggs. Reducing this risk by mating with more males could also be costly, for example due to sexually transmitted diseases. A comparable cost of mating with popular males has been found in one fish species, where females suffer reduced egg fertilization because popular males allocate less sperm per mating (Warner *et al.* 1995).

Repeated solicitation by females appears to be underpinning male mate choice in the great snipe. Several ideas exist for explaining the adaptive value for females of copulating more than once with the same male (Hunter *et al.* 1993), but few of these would apply to lekking

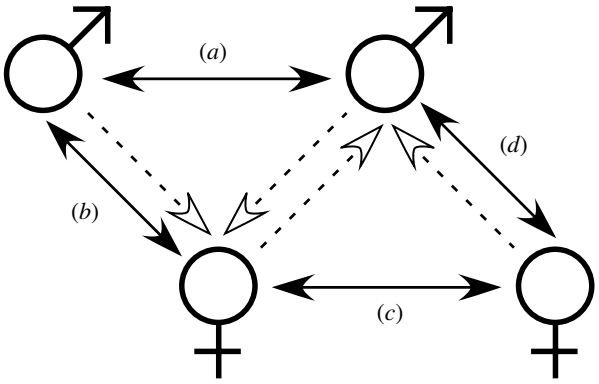


Figure 2. The conflicts of interest within and between the sexes as the outcomes of competition for mates and mate choice (see also Gowaty 1997). Dashed arrows show the individual with which a participant would benefit from copulating when unconstrained by other individuals. Double pointed solid arrows show the conflicts of interest between the parties. Adaptations arising from competition for mates should evolve because they increase an individual's pool of potential mates, whereas adaptations arising from mate choice should decrease the pool of potential mates (Wiley & Poston 1996; Widemo & Sæther 1999). Some documented behavioural adaptations in the great snipe that fit with the various conflicts are indicated below (in parentheses). (*a*) Male competition for mates (males disrupt females at neighbours' territories) (Sæther *et al*. 1999). (*b*) Female mate choice (females return to a preferred male's territories despite being repeatedly disrupted) (Sæther *et al*. 1999). (*c*) Female competition for mates (females solicit more with popular males and may disrupt other females) (Fiske & Kålås 1995; this study). (*d*) Male mate choice (popular males refuse solicitations from and chase away females with which they have already copulated) (this study).

species. One possibility is that females benefit by preventing other females from gaining good genes (Petrie 1992), although the restricted conditions for evolution of such spiteful behaviour (Hamilton 1970) renders the idea unlikely. Another hypothesis is that females copulate repeatedly in order to ensure fertilization (Birkhead *et al*. 1987; Hunter *et al*. 1993). In opposition to this it has been argued that male refusal of female solicitation is not consistent with the hypothesis (Hunter *et al*. 1993). However, this female perspective ignores the possibility that a male's interests may diverge from those of the female soliciting copulations with him. Providing the amount of sperm optimal for the female may not necessarily maximize the total fertilization success of a male. Popular great snipe males seemed to have more to gain by copulating with new females instead of remating, even if females sometimes copulate with additional males. We argue that females attempt to copulate repeatedly in order to ensure fertilization of all their eggs and may therefore sometimes be forced to mate with additional, less preferred males. This may contribute to the reason why male mating success is not always extremely skewed in this lekking species (Fiske *et al*. 1994) and may result in multiple paternity in broods. Despite this potential cost of sperm competition of being choosy, the results indicate that there may be diminishing returns for males from repeated copulations with the same female.

Two factors could therefore incur costs of being choosy for a male: unfertilized eggs and sperm competition, but we expect these costs to be relatively small compared with the benefits. A male with limited sperm may benefit more from inseminating new females rather than repeatedly inseminating the same female. Constraints on sperm availability in popular males may hence offer an evolutionary explanation for both competition among females and male choosiness, although this remains to be tested directly.

Great snipe males not only refused to copulate, but also violently chased females with which they had already copulated away from their territory. Males may perhaps expel these females in order to prevent them from interfering with other females willing to mate or to prevent the attraction of interfering neighbour males (Sæther *et al*. 1999). In any case, this provides independent support for the idea that male reluctance to remate is not due to some confounding factor or artefact of copulating in itself, but rather because males are choosy.

The basis for male mate choice in the present case appears to be solely derived from non-genetical variation in 'quality' among females because of state-dependent variation in the value of an individual female for a male. Hence, there seems to be no scope for the evolution of traits in females by sexual selection that is caused by direct male preferences for such traits. However, male mate choice may still create a context for the evolution of female traits, such as competitive behaviour, that lessen the costs for a female of male choosiness by affecting the options available for males. An interesting evolutionary interplay thus emerges where male mate choice and female competition for mates may influence each other.

The results of the present study and previous analyses in the great snipe on female copulation behaviour (Fiske & Kålås 1995) and male disruptive behaviour (Sæther *et al*. 1999) suggest that behavioural adaptations have evolved in response to four distinct but interacting (Birkhead & Møller 1998; Alonzo & Warner 1999) conflicts of interest over copulations (figure 2). The prevailing view of lek mating females being unconstrained by other females in obtaining copulations has previously been challenged (Petrie *et al*. 1992; Berglund *et al*. 1993) and our study also calls for reconsideration of the kinds of mating conflicts affecting lekking males.

In conclusion, although males of the lekking great snipe are highly competitive and females are very choosy (Sæther *et al*. 1999), their sex roles are more complex. Sexual conflicts also appear to have resulted in female competition and male choosiness, probably due to limitations on the males' sperm supply because females copulate repeatedly.

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